BIOSYSTEMATICS OF THE TEXANAE VERNONIAS (VERNONIEAE: COMPOSITAE)[1]

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ABSTRACT. In the most recent monograph of *Vernonia* in North America, this species-group was treated as four species (*V. texana*, *V. greggii*, *V. schaffneri*, and *V. ervendbergii*). Information from ecological observations, comparative morphology, biochemical systematics, transplant studies, hybridization experiments, and geographical distribution is presented and used to establish a new classification. Two species are now recognized in the group: *V. texana*, from the south central United States, and *V. greggii* with four subspecies from the Sierra Madre Oriental in Mexico.

INTRODUCTION

The genus *Vernonia* Schreb. is largely tropical with about 800 to 1,000 species distributed both in the Old and in the New World. Gleason (1906) divided the North American members of section *Lepidoploa* into two subsections and seven series. The species from the eastern United States and northeastern Mexico were included in subsection *Paniculatae* series *Verae*. Gleason recognized a number of species-groups within series *Verae*, each characterized by its own morphological features and geographical distribution. Four species were included in the Texanae species-group: *V. ervendbergii* Gray, *V. greggii* Gray, *V. schaffneri* Gray, all from the Sierra Madre Oriental of northeastern Mexico, and *V. texana* (Gray) Small, from the south-central United States (Gleason, 1906, 1922). The loose inflorescences, the hemispheric to broadly campanulate involucres, and the southwestern distribution characterize this group (Gleason, 1906).

Gleason (1923) suggested that the North American Vernonias could be traced back to an origin in South America. His theory was based on the increase toward the south in the number of species and on what he considered to be the more primitive morphology of the tropical species. He theorized that *Vernonia* followed two migration routes into North America. The eastern route was through the Windward Islands into the Greater Antilles. The western route was through Central America and Mexico into the southwestern United States through Texas and, hence, north into the eastern one-half of the United States. Gleason (1923) believed that the Texanae

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species-group is the most primitive in series *Verae*.

The taxonomic history of the group is not complicated. Torrey and Gray (1841) cited a λ form of *Vernonia angustifolia* Michx. as having leaves which were longer than the α and β form. Also, they recognized the form as occurring in Louisiana and Texas, while the α and β ranged from Florida to North Carolina. Gray (1844) followed the earlier treatment of Torrey and Gray (1841) for *V. angustifolia* var. *texana*. He separated this variety primarily on the shape of the involucral bract tips. Trelease (1888) changed the name of *V. angustifolia* to *V. granienifolia* (sic) var. *texana* in Branner and Coville's (1891) "Plants of Arkansas"; however, *V. gramienifolia* is a later homonym. Kuntze (1891) changed the generic name of *Vernonia* to *Cacalia* and applied the name *C. angustifolia* var. *texana* to a specimen from Cairo, Mississippi, located in the extreme northeastern corner of the state. Twelve years later Small (1903) elevated var. *texana* to the rank of species.

Vernonia ervendbergii and *V. schaffneri* were described as species by Gray (1882) in his "Novitiae Arizonicae". In this same publication Gray recognized two extremes of *V. greggii* as var. *greggii* and var. *palmeri*. Eighteen years later, Gleason (1906) eliminated var. *palmeri*, and in 1937, Standley described *V. taylorae*; a name that has more or less been ignored. Throughout the experimental sections of this study, *Vernonia ervendbergii*, *V. greggii*, *V. schaffneri*, and *V. texana*, are referred to *sensu* Gleason (1922).

There has been a great deal of confusion and uncertainty with regard to the identifications of the three species from Mexico. This lack of understanding is due primarily to their similar morphology and to lack of collections. There also has been some difficulty in identification due to hybridization between *Vernonia texana* and several sympatric species in the United States. The chromosome numbers for *Vernonia greggii* and *V. texana* have been previously reported as n = 17 by Hunter (1964) for the former and by Jones (1970) for the latter. The chromosome numbers of *V. schaffneri* and *V. ervendbergii* have not been previously reported. Experimental hybrids had not been made previously between Vernonias from the United States and Mexico.

The purposes of this study were: (1) to investigate their cytotaxonomy; (2) to determine whether or not the Mexican Texanae could be intercrossed with each other and with other members of series *Verae* native to the United States; (3) to better delimit the geographical ranges of the Mexican taxa; and (4) to develop a taxonomic treatment of the group based upon results from anatomical, biochemical, cytological, ecological, hybridization, and morphological studies.

RESULTS

Anatomy and morphology. The upper and lower leaf blade epidermis, leaf trichomes, leaf venation, leaf anatomy, pollen grains, achenes and pappus were compared among all four taxa (cf. Appendix). The observed differences in these features were slight among the taxa. Leaves of *Vernonia texana* have two palisade layers whereas the three Mexican taxa have a single palisade layer. The achenes of *V. texana* tend to be densely covered with trichomes whereas the others are not. The anatomy and morphology of the three Mexican taxa are quite similar and in general resemble that found in the other members of subsection *Paniculatae* series *Verae* (Jones, 1972; Urbatsch, 1972; Faust, 1972; King and Jones, 1975).

Chromosome numbers. Acetocarmine squashes of pollen mother cells from 26 collections of the four taxa all yielded $n = 17$ (cf. Appendix). These additional counts confirm earlier reports (Hunter, 1964 and Jones, 1970) and conform to that found in series *Verae* in eastern North America.

Chemotaxonomy. Flavonoids were examined from 31 populations (cf. Appendix) of these four taxa. There was some variation in compounds among the local populations of *Vernonia texana* but all four taxa have the same flavonoid compounds. The flavonoid variation in *V. texana* seems to be in part geographical and also due to hybridization with other sympatric taxa. The taxa of this study have the greatest number of flavonoid compounds in series *Verae* (Mabry *et al.*, 1975). If reduction in compounds is an advanced feature then the flavonoid evidence supports Gleason's (1923) hypothesis that the Texanae species-group is primitive in series *Verae*. Mabry *et al.* (1975) report that all taxa have the sesquiterpene lactone glaucolide-A.

Experimental hybridizations. Crossing experiments of the Texanae species group with other species in series *Verae* gave 80 to 90% mean pollen stainability in F_1, F_2, and F_3 generations. Details of the 154 crosses attempted in 105 combinations of taxa are reported in Chapman (1973) [Xerox copies are available from G.C.C.]. Generally highly fertile (as indicated by pollen stainability) first, second, and third generation and backcross hybrids were obtained. Some of the progeny from the second and third generation hybrids were weak and had abnormal development similar to that reported by Faust (1972), but no significant hybrid sterility barriers were observed. One of the more significant aspects of this study is that the taxa of series *Verae* from the Sierra Madre Oriental of northeastern Mexico can be crossed with other Vernonias from the eastern United States despite many years of geographical isolation. Hybrids between the Mexican Texanae and members of the Mexican series *Umbelliformes* produced hybrids with ca. 20–25% stained pollen (Jones, 1976).

Morphological analysis of local population samples. Local population samples of ten to twenty-six plants were collected from several locations throughout the ranges of each taxon (see Fig. 1). Twelve morphological characters (see Table 1) were measured on each plant of the population samples and the values obtained were punched onto computer cards. The mean, standard deviation, and range of each character for every population was calculated, using a BMDO2R—Step-wise Regression Program from the Health Sciences Computing Facility, UCLA (April 13, 1965 version). A multivariant, univariant discriminant analysis of irregular data program

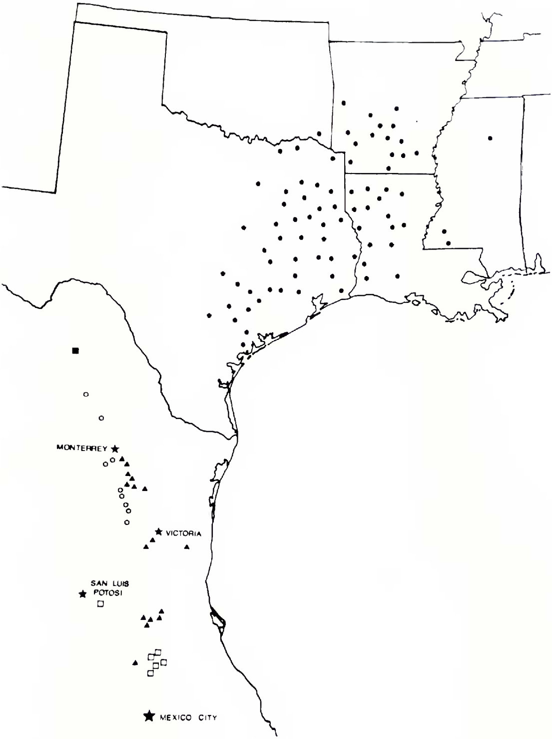

Fig. 1. Distribution of *Vernonia texana* (closed circle); *V. greggii* ssp. *greggii* (open circle), ssp. *ervendbergii* (triangle), ssp. *schaffneri* (open square), and ssp. *faustiana* (closed square).

(MUDAID—6400) written by Dr. R. E. Barghman of the University of Georgia Statistics Department was used to compare these four taxa. Individual populations of a taxon were combined into a single group for the computer analysis. For example, the *Vernonia ervendbergii* group contained 75 individual plants from 3 population samples; *V. greggii*, 100 (4 populations); *V. schaffneri*, 97 (4 populations); and *V. texana*, 389 (18 populations). In addition, the features of each taxon were compared, using dice-grams for each of the twelve characters. Polygonal graphs showing eight characters were constructed for each population and overlaid on or near their collection site on a base map. A hybrid population of *V. texana* was analyzed with scatter diagrams.

It was assumed that much of the variation among the species-group and certain correlations of characters might be better understood if only the three Mexican taxa were analyzed together. Hence, another analysis was made that excluded *Vernonia texana* using the same MUDAID—6400 program as before. The MUDAID program included a canonical test of correlation for each of the twelve morphological characters to each other and a comparison of each character to the standard error.

The results shown in Table 2 indicate that the number of flowers/head is the most useful character to distinguish the populational means of *Vernonia texana*, *V. ervendbergii*, *V. greggii*, and *V. schaffneri*. The next best characteristic is involucre length, followed in decreasing order by inner bract length, involucre width, leaf width, leaf length/width, outer bract length, inner bract width, outer bract width, leaf length, outer bract length/width, and inner bract length/width. When *V. texana* is removed from the statistical comparison, there is a shift in the order of significant characters. For example, in the comparison without *V. texana*, the inner bract is the most significant character and the number of flowers per head dropped to the fourth best character.

The variation pattern in eight characters of 24 populations of *Vernonia texana* from throughout most of its geographical range is shown by poly-

TABLE 1. Morphological Characters Measured or Scored on the Local Population Samples.

Characteristic	Characteristic
(LELT) Leaf length, mm	(IBL) Inner bract length, mm
(LEWI) Leaf width, mm	(IBW) Inner bract width, mm
(LL/W) Leaf length/width	(IL/W) Inner bract length/width
(INLT) Involucre length, mm	(OBL) Outer bract length
(INWI) Involucre width, mm	(OBW) Outer bract width
(FLS) Flowers per head	(OL/W) Outer bract length/width

gonal graphs in Figure 2. Of the eight characters used in the polygons, leaf width and leaf length/width appear to vary the most from population to population. Leaves tend to be narrower in the southeastern part of the range and wider toward the north and northwest. Much intra-populational variation is revealed in the polygons, and no definite geographical correlation is apparent.

The polygonal graphs constructed from sixteen population samples of the three Mexican taxa, *Vernonia ervendbergii*, *V. greggii*, and *V. schaffneri*, are compared in Figure 2. There appear to be no major differences in their basic shape, but there is a considerable difference in the size of the graphs. The eastern side of the Sierra Madre has the smallest polygons, the western side has the largest, and to the south are found the intermediate polygons showing a geographical correlation.

The dice-grams (Figure 3) demonstrate that the ranges of all twelve characters overlap when composite populations of *Vernonia ervendbergii*, *V. greggii*, *V. schaffneri*, and *V. texana* are compared.

The MUDAID computer program produced a table showing correlations based on matrix E (correlation based on corrected Σ from ANOVA) among the twelve characteristics used in the morphological studies. Table 3 presents each character and the five characters most correlated with it for all four taxa, *Vernonia texana*, *V. ervendbergii*, *V. greggii*, and *V. schaffneri*. Those characters showing a value of .500 or higher are considered significant and are underlined. The inner bract length shows a correlation between

TABLE 2. F *vs.* Standard Error for Characteristics Measured on Local Populations of the Texanae Species—Group of *Vernonia*.

Mexican Taxa		Mexican Taxa + *V. Texana*	
Character*	F Value	Character*	F Value
IBL	197.6	FLS	750.3
INWI	193.4	INLT	613.8
INLT	181.3	IBL	368.0
FLS	169.7	INWI	365.1
OBL	144.0	LEWI	305.4
LL/W	89.4	LL/W	192.6
LELT	67.6	OBL	155.9
OBW	60.9	IBW	103.6
IBW	27.6	OBW	70.6
LEWI	17.9	LELT	54.2
IL/W	17.5	OL/W	16.0
OL/W	13.0	IL/W	10.0

* Refer to Table 2 for explanation of abbreviation.

the involucre width, inner bract width, inner bract length/width, and outer bract length; the inner bract width to the inner bract length/width and the outer bract length to the outer bract width.

Natural hybridization between *Vernonia texana* and *V. baldwinii* is documented by scatter diagrams in Figure 4. The hybrid population sample (15843) includes some of both parental types and many intermediate forms. Putative backcrosses were also recognizable within the population. Artificially produced F_1 hybrids (crosses 10C, 11C) are morphologically intermediate between the two parental types, *V. texana* (15839) and *V. baldwinii* (15841).

The morphological analysis of the local population samples indicates that *Vernonia ervendbergii*, *V. greggii*, and *V. schaffneri* are related to *V. texana*; however, *V. texana* can be easily distinguished from the other three taxa. The smaller number of flowers per head and the narrow-linear to narrow-lanceolate leaves of *V. texana* are the most useful key characters for separating *V. texana* from the three Mexican taxa. It is not possible to clearly separate the three Mexican taxa from each other with morphological features.

The morphological characters evaluated for the local population samples of *Vernonia texana* vary in their mean values as shown by the polygonal graphs. This variation can be expected since the taxon ranges over a rather

TABLE 3. Correlation of the Five Most Correlated Characteristics Based on Matrix E for *Vernonia ervendbergii*, *V. greggii*, *V. schaffneri*, and *V. texana*.

Character*	Correlation				
	Higher				Lower
LELT	LEWI .388	INWI .133	IBW .108	OBW .102	FLS .092
LEWI	LL/W .492	LELT .388	OBW .320	OBL .276	INWI .232
LL/W	LEWI .492	OBL .265	OBW .261	INWI .196	IBL .160
INLT	IBL .371	OBL .299	FLS .278	OBW .201	LEWI .128
INWI	IBL .509**	FLS .384	OBL .350	LEWI .232	IL/W .212
FLS	INWI .384	INLT .278	OBL .264	IBL .241	OBW .220
IBL	OBL .624	IL/W .539	INWI .509	INLT .371	OBW .313
IBW	IL/W .779	OBW .312	OL/W .248	LEWI .186	FLS .172
IL/W	IBW .779	IBL .539	FLS .396	OL/W .345	OBL .285
OBL	IBL .624	OBW .557	OL/W .397	INWI .349	INLT .299
OBW	OBL .557	OL/W .397	LEWI .320	IBL .313	IBW .312
OL/W	OBL .397	OBW .397	IL/W .345	IBL .277	IBW .248

* Refer to Table 2 for explanation of abbreviation.

** Underlined characters show high correlation.

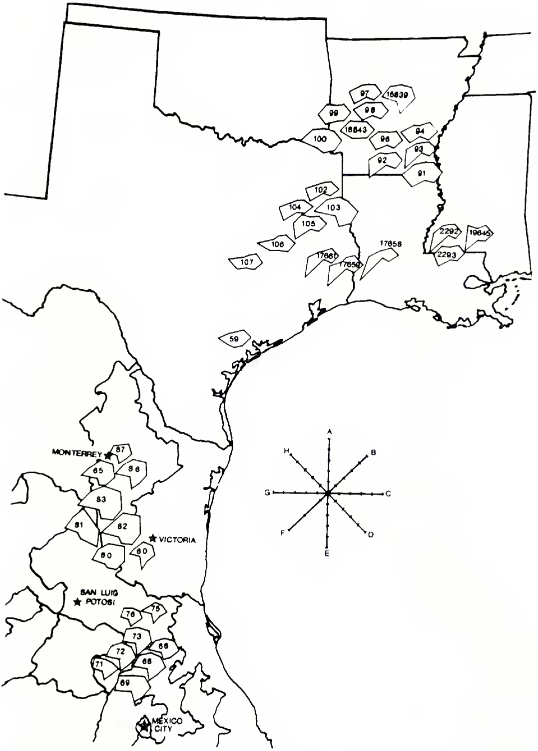

Fig. 2. Polygonal graphs of eight morphological characteristics from local populations of *Vernonia texana* (in U.S.) and *V. ervendbergii*, *V. greggii*, and *V. schaffneri* (in Mexico). The number inside polygon is a collection number (cf. Appendix). Axes represent A, number of flowers per head; B, involucre length (mm); C, inner bract length (mm); D, involucre width (mm); E, leaf width (cm); F, leaf length/width; G, outer bract length (mm); H, inner bract width (mm).

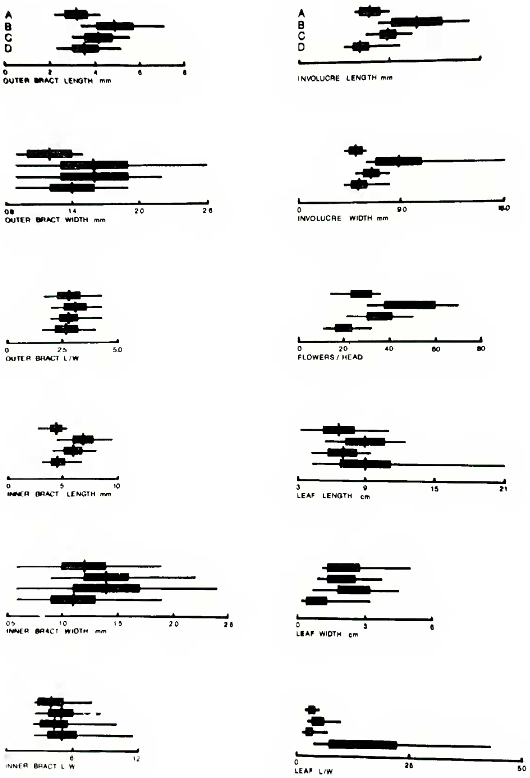

Fig. 3. Mean, range, and standard deviation for selected characters of *Vernonia ervendbergii* (A), *V. greggii* (B), *V. schaffneri* (C), and *V. texana* (D) from combined populations of each taxon.

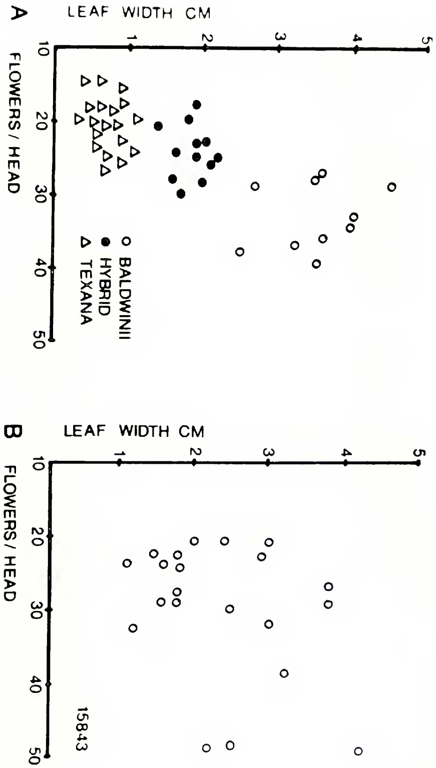

Fig. 4. Scatter diagrams of *Vernonia texana* and *V. baldwinii*. A, typical *V. texana* (15839), artificial F_1 *V. texana* X *V. baldwinii* hybrids (X10C, X11C), and typical *V. baldwinii* (15841); B, local population sample (15843) is a hybrid population which includes putative hybrids and both parental types.

large geographical area but the variation is due to natural hybridization with other sympatric Vernonias.

The eight morphological characters of *Vernonia ervendbergii*, *V. greggii*, and *V. schaffneri* compared in polygonal graphs (see Fig. 2) show some geographical correlation. Although the taxa appear sympatric, the mountainous region where these taxa occur provides diverse habitats. Two populations could be only a few airline miles apart, yet be isolated by a mountain range, with one site being dry and the other wet. The isolation available in the area would allow local populations to diverge, since they are probably not sharing the same gene pool with many adjacent populations.

The hybridization experiments demonstrated that hybridization can occur in the greenhouse and some evidence of natural hybridization is suggested by the polygonal graphs of populations *85* and *86*. These two populations are intermediate in size between those of *V. ervendbergii* (87) and *V. greggii* (83). The two intermediate populations (85, 86) were collected along a road cut through the Santa Rosa Canyon connecting the ranges of *V. ervendbergii* and *V. greggii*. Scatter diagrams of *V. greggii*, *V. ervendbergii*, and putative hybrid populations confirm that natural hybridization does occur between the Mexican taxa (Fig. 5). Most of the individuals in the hybrid population appeared to be F_1 hybrids rather than backcrosses to either parent.

Vernonia schaffneri populations generally are intermediate between *V. ervendbergii* and *V. greggii* and resemble closely the population (86) discussed above. This possibly could be the result of past hybridizations, with the hybrids now occupying slightly different habitats than either *V. ervendbergii* or *V. greggii*.

Transplant studies and ecology. In the autumn of 1970 and the summer of 1971, rootstocks of *Vernonia ervendbergii*, *V. greggii*, and *V. schaffneri* were collected from the field, potted, and grown in the greenhouse and transplanted into the Botany Plant Growth Facility Garden in Athens in the spring of 1971 and 1972. Rootstocks of *V. texana* were collected in the summer of 1971 and transplanted to the garden in the spring of 1972.

Transplants of *Vernonia ervendbergii*, *V. greggii*, and *V. schaffneri* from Mexico, and *V. texana* from the south central United States became established and were successfully over-wintered for four years at Athens until termination of the experiment. Vegetative shoots began emerging from the underground rhizomes during late April and early May. Floral development in the three Mexican taxa began in late May with some anthesis by the first week in June and by mid-June they were at the peak of flowering. The flowering period normally lasted for 3–4 weeks. *Vernonia texana* began growing vegetatively about the same time as the Mexican taxa but did not reach peak flowering until the middle of August. The garden populations of *V. texana* showed a variation of 7–10 days in the time of anthesis, with the populations from Arkansas flowering before those from southeast Texas.

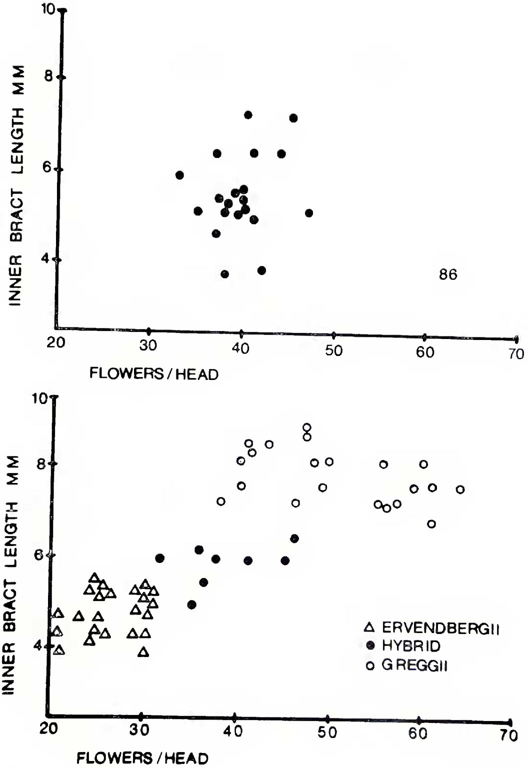

Fig. 5. Scatter diagrams of hybridization between *Vernonia greggii* and *V. ervendbergii*. Local population sample *86* (top) is a hybrid population which includes primarily hybrid type plants. The lower diagram compares typical *V. greggii* (83), artificial F_1 *V. greggii* X *V. ervendbergii* hybrids (X35C), and typical *V. ervendbergii* (87).

The Mexican taxa are found primarily in the open oak-pine vegetative zone at ca. 4500 ft to 7500 ft in the Sierra Madre Oriental on limestone parent material. They also invade semi-disturbed habitats such as roadsides or pastures and sometimes form large local populations. The soils from habitats of *Vernonia ervendbergii* and *V. greggii* are of similar pH and type. There are many exposed limestone boulders in these areas, and the soil is very dark colored with a pH of 7–8. *Vernonia ervendbergii* occupies the moist, slightly alkaline soils in the open oak-pine zone of the eastern slopes of the Sierra Madre Oriental. *Vernonia greggii* is found on the western side of the Sierras in slightly alkaline soil of the open pine zone where, due to the rain shadow, there is less moisture. *Vernonia schaffneri*, found in the extreme southern part of the species-group's range in Mexico, inhabitats severely eroded, over-grazed pastures. Much more precipitation falls in this area, as evidenced by the lush vegetation and severely eroded pastures. Some parental limestone rocks are exposed, but the soil is not as well-drained as that of *V. ervendbergii* or *V. greggii*. This soil is red with a pH of 4–5.

Vernonia texana is associated with the pine-oak communities of east Texas to Mississippi, north to the mixed hardwood forest of central Arkansas. These habitats are typically dry, on sandy soil with little organic matter and a pH of approximately 5.5. Plants of *V. texana* are widely scattered in openly grazed areas, woodlands, and along road and railroad right-of-ways.

SYSTEMATICS AND TAXONOMIC TREATMENT

Vernonia texana is uniform throughout its range in chromosome number and leaf anatomy. It is variable in a few morphological characters (leaf width and leaf length/width); however, no sharp discontinuities were detected in the morphological variation. Interspecific hybridization also causes some local morphological and flavonoid variation. The transplant studies indicated a slight variation in the phenology of local populations on a north-south gradient. Although variation was noted within *V. texana*, no distinct subpopulations that merit naming were detected.

The three Mexican taxa, *Vernonia ervendbergii*, *V. greggii*, and *V. schaffneri*, are more closely related to each other than to *V. texana*. Cytologically and phytochemically, the three Mexican taxa are identical as all have the sesquiterpene lactone glaucolide-A and the same flavonoid compounds (Mabry, *et al.*, 1975). Also, the leaf venation, trichome complement, and internal leaf anatomy are similar; nevertheless, slight variation in the leaf epidermal pattern exists among the taxa. The vegetation zone where all three taxa grow in the Sierra Madre Oriental is similar (Leopold, 1950), although their micro-habitats differ. With the exception of one character, the number of flowers per head, the three taxa are not easily distinguished from one another. The values obtained for almost all morphological characters overlapped, including the number of flowers per head. The MUDAID-6400 (discriminant analysis) program did not provide any combination of characters that clearly separated one taxon from another. There was, however, a rather distinct geographical correlation with the morphological variation.

The four taxa in the Texanae species-group are closely related. The phytochemical data, both flavonoid and sesquiterpene, was identical. There were no differences in the chromosome number or basic leaf anatomy since the same kinds of trichomes, leaf venation, and leaf epidermal patterns were found in all members of the group. A discriminant analysis of morphological characters from local population samples throughout the range of each taxon suggested that *Vernonia texana* is separable from the three Mexican taxa. In contrast, the three Mexican taxa were not distinctly separable from each other. Artificial hybridization experiments indicated that no gross chromosomal differences existed among the four taxa. Fertility was high among the F_1s, and no hybrid breakdown was found within the group. Although the habitats and geographical ranges are diverse, all taxa were able to survive for four years in a uniform garden in the Piedmont of the Southeastern United States. However, as Miranda and Sharp (1950) first suggested, the climates of the uplands of the southeastern United States and of the Sierra Madre Oriental of northeastern Mexico are surprisingly similar.

The four taxa were probably derived from a common ancestral line. *Vernonia texana* should be maintained as a species and the three Mexican taxa treated as subspecies. Since *V. ervendbergii*, *V. greggi*, and *V. schaffneri* were described by Asa Gray (1882) in the same publication, the choice of which name to apply is entirely a matter of preference for the author (Stafleu, 1972) and *V. greggii* was selected.

During the course of this study a herbarium specimen from Mexico was discovered which could not be assigned to the Mexican subspecies. The specimen's collection location (Muzquiz, Coahuila) is most interesting, since this site is directly along the likely migration route that *Vernonia* used to reach the United States (Jones, 1976). We feel that this most likely represents a different population and should, therefore, be treated as a subspecies of *V. greggii.* Ideally, a systematist should have more material on which to describe a subspecies; however, at this time this is impossible. A trip to Muzquiz was made in August 1973 to search for additional plant material of this taxon but the trip was unsuccessful due to the remoteness of the area and mechanical troubles with the vehicle.

1. Heads 11–35 flowered (usually ca. 20); middle cauline leaves 0.2–3.4 cm wide, stiff; involucres 4–9 mm high; pinelands, E Texas, SE Okla., Ark., La., SW Miss. . . . . 1. *V. texana.*
1. Heads 15–75 flowered (usually over 27); middle cauline leaves 0.7–5 cm wide, flexible; involucres 5–15 mm high; oak-pine zone, Sierra Madre Oriental . . . . 2. *V. greggii.*

1. VERNONIA TEXANA (Gray) Small, Fl. S. E. U. S. 1160. 1903.

Vernonia angustifolia Michx. var. *texana* Gray, Syn. Fl. N. Am. 1: 91. 1884. TYPE: Louisiana, *Dr. Hale s.n.* (HOLOTYPE: NY!)

Vernonia angustifolia T. & G. Fl. N. Am. 2: 59. 1841. TYPE: Louisiana, *Dr. Hale s.n.* (HOLOTYPE: NY!)

Vernonia granienifolia [sic] Walt. var. *texana* (Gray) Trel. ex Branner & Coville, Rep. Geol. Surv. Ark. for 1888. 189. 1891.

Cacalia angustifolia (Michx.) Kuntze var. *texana* Gray, Rev. Gen. Pl. 232. 1891.

Perennial herbs; stems erect, puberulent to glabrate, 4–10 dm high; leaves scattered, cauline; blades of middle stem leaves 0.2–1.4 cm wide, 6.5–13.5 cm long, linear to linear-lanceolate or sometimes lanceolate, scabrous above, scabrous to puberulent beneath, apically acute, basally attentuate, margins revolute, remotely serrate, or sometimes prominently toothed; petioles 1–4 mm long, puberulent; inflorescence loose and open; heads 15–25 flowered; involucre broadly campanulate, 4–6 mm high, 5–7 mm wide; phyllaries imbricate, slightly appressed, greenish-purple, ciliate; inner phyllaries oblong to oblong-lanceolate, 2.9–6 mm long, 1–1.7 mm wide with acute to short-acuminate tips ca. 0.1–0.2 mm long; pappus brownish to straw colored, often tinged with purple, inner bristles 5.5–7 mm long; outer scales ca. 0.6 mm long; corollas 9–11 mm long; achenes 1.5–3 mm long; flowering from late July to August; chromosome number $n = 17$.

This species is distributed from Arkansas and SE Oklahoma south to E Texas and SW Mississippi (Fig. 1).

Vernonia texana grows in well-drained soil of pinewoods and along roadsides. This species is known to hybridize in nature with *V. baldwinii*, *V. gigantea* and *V. missurica.*

2. VERNONIA GREGGII Gray, Proc. Am. Acad. 17: 204. 1882. Typification listed under subspecies.

Perennial herbs; stems erect, puberulent to glabrate, 2–10 dm high; leaves scattered, cauline; blades of middle stem leaf 0.7–5 cm wide, 3.3–12.5 cm long, lanceolate to linear-lanceolate, elliptic or ovate, scabrous above, scabrous to puberulent beneath, apically acute to acuminate, or obtuse, basally narrowed to nearly sessile, margins serrulate to remotely serrulate; petioles 1–3 mm, nearly sessile, puberulent; inflorescence loose and open, sometimes flattened; heads 14–75 flowered; involucre campanulate to hemispheric, 5–15 mm high, 4–18 mm wide; phyllaries imbricate and appressed, with acute to obtuse or long acuminate tips, glabrous to thinly ciliate; achenes 3.5–10 mm long; flowering from early June to late July; chromosome number $n = 17$.

This species is distributed throughout the Sierra Madre Oriental of Mexico (Fig. 1). The subspecies are characterized by the following key:

1. Heads ca. 75 flowered; outer phyllaries long acuminate. . . . . . . 2d. ssp. *faustiana.*
1. Heads less than 70 flowered; outer phyllaries not long acuminate.
   2. Middle stem leaves lanceolate to linear-lanceolate, heads usually over 40 flowered; western slopes of Sierra Madre Oriental. . . . . 2a. ssp. *greggii.*
   2. Middle stem leaves elliptic to ovate, heads usually less than 40 flowered; eastern slope of the Sierra Madre Oriental.
      3. Heads 27 (14–36) flowered, phyllaries greenish with purple tips, pappus whitish to straw colored. . . . . . . .2b. ssp. *ervendbergii.*

Heads 36 (21–50) flowered, phyllaries purple, pappus brownish-tawny colored. . . . . 2c. ssp. *schaffneri*.

2a. VERNONIA GREGGII Gray ssp. GREGGII

TYPE: Mexico: Nuevo Leon, valley near Saltillo, 1848, *Gregg 102* (HOLOTYPE: MO!)

Vernonia greggii Gray var. *palmeri* Gray, Proc. Am. Acad. 17: 204. 1882. TYPE: Mexico: Nuevo Leon, 1880, *Palmer 753* (HOLOTYPE: NY!)

Vernonia taylorae Standl., Field Museum Pub. Botan. 17: 224. 1937. TYPE: Mexico: Hacienda Pabillo, Galeana, Nuevo Leon, 1963, *Taylor 9* (HOLOTYPE: F!, ISOTYPE: TEX!)

Vernonia greggii ssp. *greggii* is distributed through the drier western side of the Sierra Madre Oriental from about Dr. Arroyo, Nuevo Leon, to the mountains immediately west of Monclova, Coahuila. This subspecies grows in rocky limestone soil, along roadsides in full sun, but is often found in semi-shade under sparse oak-pine-juniper forest. Sometimes robust plants are found along wet ditches or dry stream sides. This taxon is somewhat variable throughout its geographical range. The range of this taxon overlaps with the range of *V. greggii* ssp. *ervendbergii* in the Santa Rosa Canyon east of Galeana, Nuevo Leon, and hybridization has been documented from populations in this area.

2b. VERNONIA GREGGII Gray ssp. **ervendbergii** (Gray) Chapman and Jones stat. nov.

Vernonia ervendbergii Gray, Proc. Am. Acad. 17: 203. 1882. TYPE: Mexico: 25 mi SW Monclova, Coah., 1880, *Palmer 750* (SYNTYPES: GH! NY!)

Vernonia greggii ssp. *ervendbergii* grows in the oak-pine vegetation along the eastern escarpments of the Sierra Madre Oriental. Its range extends from about Monterrey, Nuevo Leon, southward to immediately north of Xilitla, S.L.P. It is also found to the east on the outlying Sierra de Tamaulipas in the Coastal Plain of Mexico. This subspecies invades semi-disturbed areas such as roadsides and cut-over forests. The soil in which it grows is black, moist, and slightly alkaline.

2c. VERNONIA GREGGII Gray ssp. **schaffneri** (Gray) Chapman and Jones stat. nov.

Vernonia schaffneri Gray, Proc. Am. Acad. 17: 204. 1882. TYPE: Mexico: near San Luis Potosi, S.L.P., 1877, *Schaffner 347* (SYNTYPES: NY!, GH!, US!)

Vernonia greggii ssp. *schaffneri* has the most restricted range of the three subspecies. This taxon is found only in the vicinity of Jacala, Hidalgo, SW of Xilitla, S.L.P., Hidalgo in the state of Queretaro, and the vicinity of Las Rusias east of San Luis Potosi, S.L.P. This subspecies seems to be associated with grazed-over pastures that are eroded into gullies. The soil is acidic, red, and gummy.

Although natural hybridization between *V. greggii* ssp. *schaffneri* and ssp. *ervendbergii* was not documented in this study, it is speculated that there may be gene flow via the mountains W of Xilitla, S.L.P. to San Luis Potosi, S.L.P. Unfortunately no roads traverse this area.

2d. VERNONIA GREGGII Gray ssp. **faustiana** Chapman and Jones ssp. nov.

TYPE: Mexico: Canyon in Sierra Hermosa de Santa Rosa, 25 mi NW Melchor Muzquiz, Coahuila, 1963, *Latorre 13* (HOLOTYPE: TEX!)

Herbe perennes erectae, 0.3–0.6 metralis, caulibus tomentosis; folia 9–13 cm longa, 1.5–2.5 cm lata, linearis-lanceolatus; scaberalus supra et infra, apicibus acutis, basibus cuneatis, marginibus dentatis, petioli 2–4 mm longi; inflorescentiae dense compactis; capitula ca. 75 florata; involucra campaniformis-hemisphericae, 9–10 mm longa, 11–15 mm lata; phyllaria imbricata, appresus, stramineo-purpurea; phyllaris interioribus linearis, 8–9 mm longis, 1.0–1.3 mm latis; phyllaris externis acumnatis longis, apicem-purpurea, 1–2 mm longis; pappi stramineus; setae interiores 7–8 mm longis; setae externae ca. 1.0 mm longis; corolla purpurea, 10–11 mm longis; achaenia fere glabris, 4–8 mm longis.

This subspecies is named in honor of Dr. W. Z. Faust, who was properly introduced to Mexico during the unsuccessful search for additional material of this taxon.

APPENDIX
COLLECTION LOCATIONS FOR SAMPLES OF *VERNONIA*

Voucher specimens (deposited in GA) of materials used in the study of flavonoids (annotated *f*), cytology (*c*), hybridization (*h*), and morphology (*m*). Collection numbers are those of the senior author unless otherwise noted.

Vernonia greggii ssp. *greggii*

MEXICO: NUEVO LEON: 2.1 mi S Pabillo, *51* (*c,f,h*); 29 mi N Dr. Arroyo, *80* (*c,f,h,m*); 30 mi N Dr. Arroyo, *81* (*c,m*); ca. 40 mi N Dr. Arroyo at LaJoya, *82* (*c,f,m*); 18 mi S Galeana, *83* (*c,m*); 9 mi E Galeana, *85* (*m*); 14 mi E Galeana, *86* (*m*).

Vernonia greggii ssp. *ervendbergii*

MEXICO: NUEVO LEON: Horsetail Falls, *45* (*c,f,h*); Horsetail Falls, *87* (*c,f,h,m*).—QUERETARO: 15 mi S Jalpan, *71* (*c,m*). Km 226, hwy. 120, 15 mi N Landade Matamoros, *72* (*m*).—SAN LUIS POTOSI: 20 mi W Valles, *75* (*c,m*); Km 71, 42 mi W Valles, *76* (*c,m*).—TAMAULIPAS: Km 153, hwy. 101, Victoria, *46* (*c,f,h*); km 153, hwy. 101, Victoria, *60* (*m*).

Vernonia greggii ssp. *schaffneri*

MEXICO: HIDALGO: 5 mi S Jacala, *49* (*c,f,h*); Km 111, hwy. 85, Puerto La Zorra, *66* (*c,f,m*); 10 mi S. Jacala, *68* (*c,m*); 17 mi S Jacala, *69* (*m*).—SAN LUIS POTOSI: Km 233, hwy. 120, 20 mi S Xilita, *73* (*c,m*); ca. 31 mi E San Luis Potosi, at Las Rusias, *79* (*c*).

Vernonia texana

UNITED STATES: ARKANSAS: ASHLEY CO.: 10 mi W Parkdale, *91* (*c,f,m*); 20 mi W Parkdale, *92* (*f,m*). CLEVELAND CO.: 8 mi N New Edinburg, *94* (*m*). DALLAS CO.: 1 mi S Princeton, *96* (*f,m*). HOT SPRING CO.: near DeRoche, *97* (*f,m*); 3 mi E Bismarck, *98* (*f,m*); ca. 9 mi NW Malvern, *Jones 15839* (*c,f,h,m*); ca. 9 mi MW Malvern, *Jones 15840* (*f*); ca. 9 mi NW Malvern, *Jones 15842* (*f,m*); ca. 9 mi NW Malvern, *Jones 15843* (*f,m*). *POLK CO.*: 5 mi N Grannis, *99* (*f,m*); 2 mi N Grannis *100* (*f,m*).—LOUISIANA: VERNON Pa.: 3 mi N Slagle, *56* (*c*); 5 mi N Leesville, *Jones 17658* (*f,h,m*).

—MISSISSIPPI: AMITE CO.: 1.3 mi E Lincoln—Amite Co. line, *Jones 2293* (*m*). FRANKLIN CO.: Clear Springs Lake, *Jones 2292* (*c,h,f,m*). PIKE CO.: 4 mi N Magnolia, *Jones 19645* (*c,h,m,f*).—TEXAS: CHEROKEE CO.: 2 mi N Jacksonville, *104* (*f,m*); 8 mi N Jacksonville, *105* (*c,m*). COLORADO CO.: 7 mi W Columbus, *90* (*c,f*). GOLIAD CO.: 10 mi SW Victoria, *59* (*c,f,m*). JASPER CO.: 6 mi NE Burkeville, *Jones 17659* (*c,f,h,m*). LEON CO.: 1 mi N Buffalo, *106* (*f,m*). MILAN CO.: 13 mi N Rockdale, *107* (*c,f,m*). RUSK CO.: 4 mi NW Tatum, *102* (*f,m*); 12 mi SW Tatum, *103* (*f,m*). TYLER CO.: 5 mi W of Woodville, *Jones 17661* (*f,m*).

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